SKELETAL STRUCTURE, DEVELOPMENT AND ELEMENTAL COMPOSITION OF THE ORDOVICIAN TREPOSTOME BRYOZOAN *PERONOPORA*

by DAVID R. HICKEY

ABSTRACT. ED spectroscopy of Ca and other elemental densities indicate differences in the rates of secretion and growth among crystallite ultrastructures, acanthostyles, the median lamina, zooecial wall, and stages of ontogeny and astogeny in *Peronopora*. Growth rate (inversely proportional to Ca density) was highest within the granular skeleton of the median lamina and 'A-type' acanthostyles (paurostyles). Growth rate decreased exponentially from the median lamina through the recumbent zone, endozone, and exozone. Paurostyle cores were deposited more rapidly than endozonal wall but less rapidly than recumbent zone wall and the median lamina. Zones of disordered irregular crystallites and laminar growth alternate in zooecial wall axes, and were respectively linked with increased secretion rates and increased episodicity during the cystiphragm/mesozooecial tabulae emplacement cycle. Cu and Mn densities support the sequence of relative growth rates inferred from the Ca data. Paurostyles and the median lamina contain more Cu than other structures. Mn is also most abundant in the median lamina and declined monotonically with reduced growth rate. The median lamina is structurally continuous with the basal lamina but was not secreted against cuticle. Formation of the median lamina and paurostyle cores may be explained by differentiation of inner epithelium for high rates of secretion.

BRYOZOAN skeletal ultrastructures, if not diagenetically altered, are most informatively viewed as products of the physiology of growth (Sakagami *et al.* 1984; Sandberg 1977, 1983; Tavener-Smith and Williams 1972). This study seeks to link differences in the skeletal ultrastructure of *Peronopora vera* Nicholson and *P. decipiens* Rominger to the rates and modes of growth of astogenetic sequences and skeletal structures. The ultrastructures of zooecial wall 'flanks' (that region of proximally directed laminae lateral to the wall axis) and axes, acanthostyles (acanthopores), and the median lamina ('mesotheca' of other authors; 'median wall' of Boardman 1983) are described by means of SE microscopy and analyzed for compositional differences by means of ED spectroscopy. Results of this study provide information about the relative growth rates of skeletal structures and astogenetic zones which can be extended to other taxa and used as bases for hypotheses concerning the evolution of skeletal structures.

The term 'granular' has been applied to two similar crystallite morphologies in many studies of skeletal ultrastructure (e.g. Tavener-Smith and Williams 1972). Both types lack regular crystallite surfaces. The term 'granular' is herein applied to large, approximately equidimensional, non-tabular crystallites that appear optically hyaline and homogeneous. The term 'irregular' is applied to smaller, non-tabular crystallites which are optically differentiable, irregular, and variable in dimensions and shape.

Much of the ultrastructure of bifoliate *Peronopora* resembles that of other trepostomes described by Tavener-Smith and Williams (1972), Tavener-Smith (1969*a*), Armstrong (1970), Bigey (1979, 1982), and Bigey and Lafuste (1982). However, the median lamina of bifoliate *Peronopora* is an unusual and distinctive structure among trepostome genera; it is otherwise found only in *Polyteicus* Pocta, *Diplostenopora* Ulrich and Bassler, *Stenocladia* Girty, *Nipponostenopora* Sakagami, *Petalotrypa* Ulrich, rare variants of *Amplexopora thomesi* Ross, and *Araxopora* Morozova. A similar

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structure is an important synapomorphy of bifoliate cryptostomes and many fistuliporines. Trepostome median lamina ultrastructure has been studied only in *Peronopora compressa* Ulrich (Tavener-Smith and Williams 1972) and *Petalotrypa* sp. (Bigey 1979). The astogenetic origin and ultrastructure of the median lamina has an important bearing on the growth mode of trepostomes (Tavener-Smith and Williams 1972) and the evolutionary origin of *Peronopora* (Hickey, in press). Additional observations demonstrate that the median lamina of the primary frond is structurally continuous with the basal lamina ('epitheca' of other authors) but is none the less interior-walled skeleton. The median lamina contains style-like structures (Boardman and Utgaard 1966) which optically resemble acanthostyle cores but differ in ultrastructure. The styles and granular layer of the median lamina exhibit ultrastructural details as yet unreported in the mesothecal skeleton of other taxa.

Few studies of the elemental composition of bryozoan skeletons have been undertaken. Phillips (1922) reported Cu, Zn, Fe, and Mn in one Recent bryozoan. Clark and Wheller (1917) found Si, Al, Fe, Mg, P, and S in a survey of 9 Recent bryozoans. Schopf and Manheim (1967) reviewed the chemical composition literature and reported Ca, Mg, Sr, Ba, Fe, P, Zn, and C in 29 Recent bryozoan species. Soulé and Soulé (1981) analyzed heavy metal uptake in 7 Recent bryozoa and discovered traces of Fe, Cr, Hg, Ni, and Zn in exoskeletons, Fe and Hg in tissues and As, Cd, Cr, Cu, Fe, Hg, Mn, Ni, Pb, and Zn in bulk samples. Morrison and Anstey (1979) provide one of the few studies of the elemental composition of fossil bryozoans. They detected C, Fe, S, Si, Al, and K in the brown bodies of *Heterotrypa* Nicholson and *Peronopora*.

Minor and trace elements, aside from Mg and Sr, have received little attention in biogeochemical studies of bryozoans or other organisms. Most studies have sought correlations between composition and temperature or salinity variation in bivalves (e.g. Dodd 1967; Eisma *et al.* 1976; and others), or links between mineralogy and phylogenetic affinities among bryozoans (Schopf and Manheim 1967). A few studies have focused on ontogenetic variation of elemental abundances in bivalves (Crisp 1975, 1983; Goreau 1977; Rosenberg 1980; Rosenberg and Jones 1975). The latter aspect of skeletal chemistry could provide data pertinent to studies of the physiology of skeletal secretion and growth in bryozoans. No compositional studies of this kind have been undertaken with fossil bryozoans. However, Sakagami *et al.* (1984) have defined categories of skeletal composition indicative of equilibrium and nonequilibrium skeletal formation in some Recent and fossil bryozoans. They concluded that the presence of Mn, Fe, Zn, Co, Cu, and Ni within cheilostome skeletons was a product of physiological control over skeletal composition.

Mg, Cu, Fe, Mn, Si, Yb, and Nb were found in *P. vera* Ulrich. This investigation is concerned with the systematic variations of Ca and trace element concentrations during astogeny and relative element abundances among major skeletal components and different microstructures. The abundance distribution of Ca, usually ignored in compositional analyses (Rosenberg 1980), is of particular interest in this study. Ca abundance could provide a measure of relative rates of skeletal and crystallite growth (Rosenberg, pers. comm. 1984). EDS analyses of Ca indicate that relative skeletal growth rates decreased with increasing age from the median lamina through the exozone. Granular crystallite morphologies typical of the median lamina and acanthostyles are indicative of higher growth rates than crystallites comprising laminar wall. The median lamina was deposited most rapidly. The development of the median lamina may be explained in terms of the differentiation of inner epithelium to produce regions of increased, and relatively continuous crystallite secretion. Acanthostyles were deposited more rapidly than endozonal and exozonal skeleton. Differences in individual crystallite shape, thickness, orientation, and laminae number suggest differential growth rates and episodicity between zooecial wall flanks and axes and cyclical zonation within axes. Exterior-walled skeleton (Boardman *et al.* 1983; 'single-walled' skeleton of many authors) of the basal lamina is inferred to have been deposited more rapidly than most interior-walled (Boardman *et al.* 1983; 'double-walled' skeleton of many authors) skeleton.

Astogenetic trends and differential abundances of trace elements could reflect the effects of growth rates (Rosenberg 1980), or other aspects of physiological change during astogeny. The abundance variations of Mn, Cu, and Fe among skeletal structures and astogenetic zones support

the inferences based on Ca abundance. Results support the inferences concerning relationships between skeletal ultrastructures and growth rates proposed by Tavener-Smith (1969*a*, *b*; 1975).

If similar crystallite morphologies in the interior-walled skeleton of other trepostome taxa are not products of alteration, the evolution of differences in zooecial wall structure among astogenetic zones and acanthostyle microstructures among closely related taxa could be interpreted in terms of heterochronic processes. Studies of compositional differences among astogenetic growth zones provide a basis for the construction of growth curves for taxa like *Peronopora* that possessed periodically deposited intrazooecial structures such as cystiphragms. Results also suggest that the evolution of mesothecal structures in other taxa involved a differentiation of inner epithelium crystallite secretion rates along the colony margin.

MATERIALS AND METHODS

Specimens used in this study belong to *P. vera* and *P. decipiens* from the Kope (Eden Shale) and Dillsboro Formations of the Cincinnatian Series (Late Ordovician) from the Ohio Valley region. Several preparation methods were used in the SEM investigation. Specimens were either fractured, or etched in 0·1% formic acid for 60–90 seconds or 1·25% EDTA for 30 minutes. Electron micrographs of acetate peels were also made. Specimens were coated with gold-palladium or carbon. Etched specimens were carbon coated for energy dispersive X-ray (EDS) analysis of elemental composition.

Electron micrographs were taken with an ISI (International Scientific Instruments) S-III SEM and the EDS analyses were made with a JSM-35C SEM, manufactured by Japan Electron Optics Limited. The latter machine is equipped with a dual annular photolithographic disc back-scattered electron detector and a Tracor Northern Energy Dispersive X-ray analysis system. EDS analyses were done at 20 kv, over time intervals of 60 seconds. Beam strength was held constant to prevent systematic bias in the relative abundance measures. Possible biases due to the variable surface topography of etched specimens are believed to have been minimal (Flegler, Director, MSU Electron Optics Center, pers. comm.). Analyses were limited to elements with atomic numbers above that of carbon because specimens were carbon coated.

Two elemental analyses were made. Changes in element abundances were measured with a narrow beam probe in a proximo-distal series of thirty-seven points taken alternately from laminar regions of the zooecial wall axis, and from cystiphragms periodically emplaced along the wall of a single zooecium. This analysis was designed to determine if there exist any elemental abundance periodicities associated with the cycle of cystiphragm emplacement. A second analysis was performed to determine if elemental abundances differed in systematic manners among astogenetic growth zones and among different skeletal structures. Abundances were measured with a line scan at magnifications of 1,000 to 9,000 for the exozone, endozone, acanthostyles, recumbent zone, and median lamina for each of fifteen zooecia of a single specimen. Magnifications that differ by less than an order of magnitude should not have a significant effect on measured abundances (Flegler, pers. comm.). Only the latter analysis provides replicate data amenable to statistical treatment and reliable inference. Mean elemental abundances were statistically compared among skeletal structures and among astogenetic zones. The Student's t-test was used to evaluate differences in the mean abundances; it was preferable to other parametric tests because sample sizes were small ($n \leqslant 15$).

Skeletal structures and different crystallite ultrastructures, as well as matrix, could respond differentially to diagenesis. Trace element distributions may be greatly influenced by the distribution and abundance of organic material in the earliest stages of diagenesis following burial. Mean abundances within skeletal structures were statistically compared with those of the zooecial void cement in order to determine whether diagenetic alteration significantly influenced skeletal composition. Some idea of the effects and extent of diagenesis on the results of this study is indicated by comparisons between element concentrations within the diagenetic zooecial void matrix and individual skeletal elements. Several elements are significantly enriched within and among various skeletal structures in comparison to mean levels found in the void cement.

Distributions of Ca and some of the trace elements are consistent with independent predictions of compositional behaviour which would be expected in the relative absence, or limited influence of diagenesis on skeletal material. Of these, Mn, Fe, and Cu occur in cheilostomes with nonequilibrium growth (Sakagami *et al.* 1984) and are thus inferred to have been little influenced by diagenesis. Yet, a differential response of skeletal materials to diagenesis and/or the effects of early-stage diagenesis could have affected the observed variations and trends. Thus, any conclusions regarding astogenetic trends and structural differences are tentative and subject to confirmation by additional studies and alternative methods.

SKELETAL STRUCTURE

The autozooecia of bifoliate *Peronopora* are subcircular to circular in cross-section, short, and arranged in fairly well defined longitudinal ranges. Recumbent zones are well developed where autozooecia diverge from either side of a median lamina (if present) in bifoliate species (Boardman and Utgaard 1966). The median lamina is a distinctive intracolonial structure, unusual among trepostomes. Cystiphragms form continuous overlapping series throughout the autozooecial tubes. The area subtended by cystiphragms decreases monotonically during autozooecial ontogeny. Cystiphragm overlap increases distally as size and spacing decrease. Acanthostyles are generally abundant, large, and may inflect autozooecial walls. The polygonal mesozooecia (mesopores) may be abundant, large, and closely tabulated.

Zooecial walls

The majority of the interior-walled skeleton is laminar, like that typical of most trepostomes (e.g. Armstrong 1970; Bigey 1979, 1982; Bigey and Lafuste 1982; Tavener-Smith 1969*a*; Tavener-Smith and Williams 1972). Autozooecial and mesozooecial wall laminae are of variable thickness, length, and continuity (Pl. 78, figs. 1 and 2). Exozonal laminae may occasionally extend the length of a wall flank and intercalate with laminae from the adjacent wall in the compound wall axis. Crystallite shape and discontinuity of laminae render it difficult to define discrete, continuous laminations. The location of actual growth surfaces is therefore obscured.

Edgewise crystallite growth can also produce the appearance of a laminated wall without synchroneity of laminae and growth surfaces (Boardman and Cheetham 1969; Boardman and

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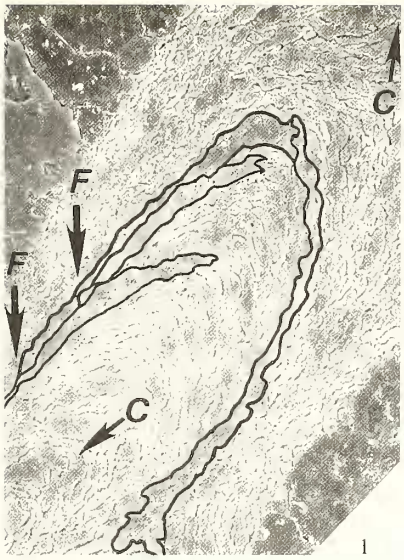
EXPLANATION OF PLATE 78

Figs. 1–8. *Peronopora vera*, Eden Shale, Ohio. 1, exozonal autozooecial wall; wall flank laminae (F) continuous with laminae comprising cystiphragm (distal to outlined laminae) and larger core crystallites (C) proximal and distal (arrows) to cystiphragm (bottom centre). Unusually long laminae and intercalation of laminae are outlined in region of wall axis between zones of larger crystallites. Long., MSU 220335-00245, Eden Shale, Ohio, × 1,000. 2, exozonal autozooecial wall. Large, irregular, disordered wall core crystallites (C) (right) proximal to wall flank laminae (F) continuous with cystiphragm (bottom left, out of field). Long., MSU 220335-00251, Eden Shale, Ohio, × 5,000. 3, pluricupular zooecial wall flank crystallites. Fractured section. Long., MSU 220335-00241, Eden Shale, Ohio, × 2,600. 4, fine ultrastructure of median granular layer. Compare granular-rhombic crystallites of median lamina with pluricupular crystallites of zooecial walls in fig. 3. Fractured section, Transv., MSU 220335-00241, × 1,000. 5, granular acanthostyle core, pluricupular crystallites of thin laminae proximal to core and larger crystallites of laminar zooecial wall to far left, right and top centre. Tang., MSU 220335-00245, Eden Shale, Ohio, × 1,000. 6, granular crystallites of acanthostyle axial core (C) and pluricupular crystallites of sheath laminae (S). Fractured section. Transv., MSU 220335-00241, × 1,500. 7, acanthostyle core and sheath laminae within autozooecial wall. Long., MSU 220335-00245, × 400. 8, acanthostyle axial core (centre) and flanking laminae. Fractured section. Transv., MSU 220335-00241, × 2,400.

Fig. 9. *P. decipiens*, median lamina; outer laminar layer (OLL), median granular layer (MGL), zooecial wall (ZW), and median styles (MS; arrows). Transv., MSU 220314-00415. Dillsboro Fm., Indiana, × 240.



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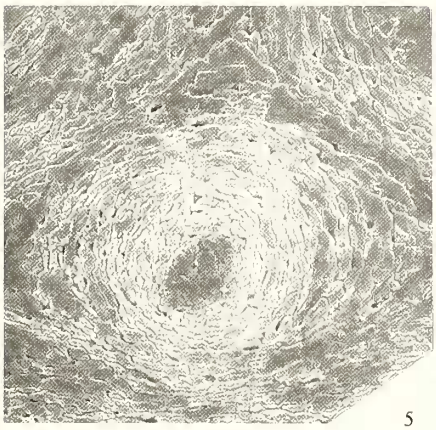
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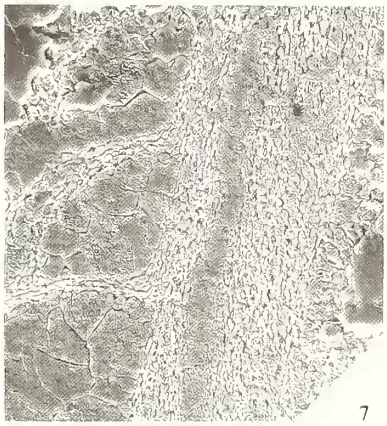
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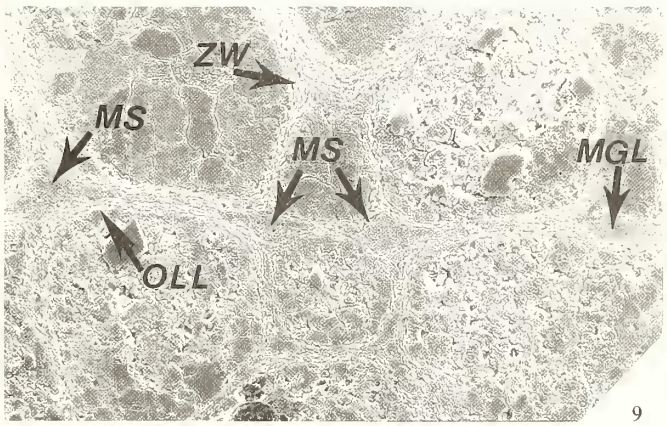

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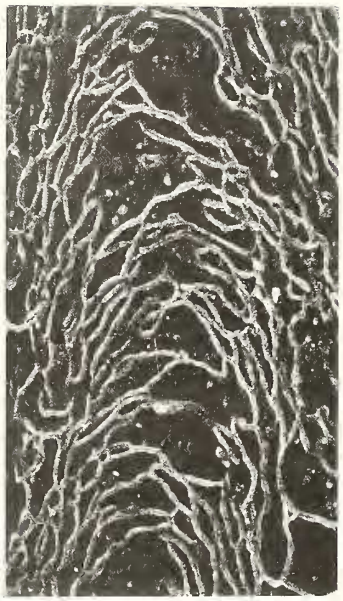


TEXT-FIG. 1. *Peronopora vera*, mesozooecial wall (axis parallel to long axis of photo) and adjoining tabula (bottom centre). Note disordered wall core and laminar flanks. Acetate peel (negative) replica. Long., MSU 220335-00239, Eden Shale, Ohio, ×2,000.

Towe 1966). Armstrong (1970) suggested the possibility of edgewise growth in *Stenopora crinita* Lonsdale. Undamaged distal tips of zooecial walls in *Peronopora* reveal continuity of laminae across wall cores with no evidence of concerted edgewise growth. Therefore structural laminae and growth surfaces are considered equivalent, and no evidence suggests non-laminar growth.

Wall laminae of cystiphragms and mesozooecial tabulae intercalate with zooecial walls and often become attenuated and terminate before reaching the wall core (Pl. 78, fig. 1). Zooecial laminae are generally thickest, and crystallites largest and most irregularly shaped within wall axes proximal to zones of laminae continuous with cystiphragms or tabulae (Pl. 78, figs. 1 and 2). Laminae which extend into zooecial walls from the distal surfaces of cystiphragms, and those typical of outer zooecial wall flanks, tend to be thinner and composed of smaller, and thinner 'pluricupular' (Pl. 78, fig. 3; see definition below) crystallites. A more pronounced alternation of axial crystallite size and shape occurs within walls shared by mesozooecia (text-fig. 1).

Wall laminae within the endozone are few in number, steeply to vertically inclined, and arch sharply over an undifferentiated, laminar wall axis (Pl. 78, fig. 9). The laminae and component crystallites throughout most of the endozone are pluricupular and somewhat larger than those of the wall flanks within the exozone. The most proximal portions of the recumbent zone are composed of granular crystallites which are short distal extensions of the median lamina (Pl. 79, fig. 4).

Crystallites

Individual crystallites of zooecial walls do not display the planar surfaces or uniform thickness and size of the tabular crystallites found in many Tubuliporata (formerly cyclostomes; Boardman 1983) and Trepostomata described by Brood (1976), Sandberg (1977), Tavener-Smith and Williams (1972), and others. For example, the laminar wall crystallites of *Stenopora* (Armstrong 1970) and *Leioclema asperum* Hall (Tavener-Smith 1969*a*) are more uniformly tabular than those of *Peronopora*. Fractured sections (Pl. 78, fig. 3) and light formic acid etches reveal that most crystallites of *Peronopora* are pluricupular-shaped like those of *Leptotrypella* Vinassa (Bigey and Lafuste 1982). Pluricupular crystallites are wafer-like tablets with undulating proximal and distal surfaces and attenuated margins (Pl. 78, figs. 1–3). Laterally adjacent crystals often exhibit intercalated, interlocking boundaries. Exozonal axial crystallites are generally larger and more

irregularly shaped than those of wall flanks (Pl. 78, figs. 1–3). Wall axes contain large, irregular crystallites which may envelop smaller crystallites. The smallest crystallites could be relicts of differential etching in response to minor compositional differences. Large irregular crystallites disrupt lamina continuity and thickness and give a generally disordered appearance to regions of the wall axis deposited between cystiphragms and tabulae (Pl. 78, figs. 1 and 2). Wall axes shared by mesozooecia appear more disordered than those of autozooecia (text-fig. 1).

Acanthostyles

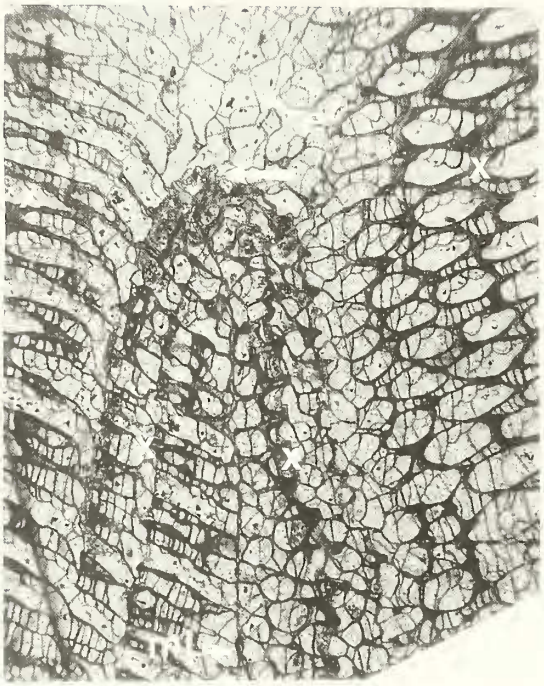
The acanthostyles of *Peronopora* have a paurostyle-like (terminology of Blake (1983) extended to trepostomes) morphology (Pl. 78, figs. 5–8). Sheath laminae (Blake 1983) adjacent to the acanthostyle axial core are composed of nearly tabular crystallites. Crystallites become thicker, longer, and more pluricupular away from the core (Pl. 78, figs. 5 and 7). Crystallites in regions of distally concave laminae between axial cores and zooecial walls are generally larger, longer, and more tabular in shape than those of zooecial walls. Fractured sections reveal large granular crystallites within the axial core (Pl. 78, figs. 6 and 8). The boundary between cores and flanking laminae is irregular yet distinct (Pl. 78, fig. 7). Laminae do not extend across the cores and no growth discontinuities were found within the core.

Median lamina

The median lamina varies in structure and continuity within and, possibly, between species. It consists of one to three components: 1, an outer laminar layer; 2, a median granular layer; and, 3, granular 'tubules' or median styles (median 'tubules' or 'rods' of other authors) (Pl. 78, fig. 9). The outer layer contains a variable number of horizontally disposed laminae composed of small pluricupular crystallites (Pl. 79, figs. 2–6). The distalmost laminae are continuous with the zooecial walls of the recumbent zone (Pl. 79, figs. 4 and 5). These laminae arch over a short distal extension of granular median lamina at the bases of zooecial junctions between adjacent walls. The median lamina may be composed entirely of two outer laminar layers, particularly in very thin walled regions and near the bases of secondary fronds. In the former case the median lamina is optically visible as a parting plane between layers of laminar skeleton separating oppositely oriented zooecia. For this reason the outer laminar layer is considered a component of the median lamina.

The median granular layer is optically hyaline, but granular in etched section (Pl. 78, fig. 7; Pl. 79, figs. 2–7). The granular layer may vary irregularly in thickness or become thin between regular lensoidal swellings (Pl. 78, fig. 9). The median layer is comprised of large, tightly interlocking granular crystallites (Pl. 79, figs. 2–6). The granules are composed of small, rhombic crystallites (Pl. 78, fig. 4; Pl. 79, fig. 1). These crystallites are broadly similar to those of the exterior walls (fixed-wall) of some cheilostomes (Sandberg 1983, figs. 121, 123–125) and the 'secondary layer' of some tubuliporates (Brood 1976; Tavener-Smith and Williams 1972). The major differences between these crystallites in *Peronopora* and those of the 'secondary layer' in tubuliporates are their lack of organization into discrete laminae, poorly defined boundaries between individual crystallites, and variable crystallite size in the former. Comparable ultrastructural detail could not be observed in the 'primary granular layer' of tubuliporates or ptilodictyines figured by Tavener-Smith and Williams (1972) or in the median lamina of the trepostome *Petalotrypa* sp. (Bigey 1979) or the cystoporate *Cystodictya* (Healy and Utgaard 1979).

The granular layer may be either internally continuous (Pl. 78, fig. 9), discontinuous, lensoidal (Pl. 79, fig. 6), or separated into segments by folding of the laminar layer around the distal end of each segment (Pl. 79, fig. 2). Segmentation of the granular layer indicates periods of slowed or interrupted growth at the frond terminus. This segmentation demonstrates the direction of growth of the medial layer and provides evidence about the location of the secretory epithelium. Regions of discontinuity and/or thinning are often associated with unusually wide zones of thin-walled ('endozonal') growth (text-fig. 2) and recumbent zooecia which lack cystiphragms (Boardman and Utgaard 1966). These observations suggest a model to explain local discontinuities in median lamina formation (see discussion). The median laminae of primary and secondary fronds are



TEXT-FIG. 2. *Peronopora vera*, discontinuity of median lamina (ml) in region of prolonged endozonal growth (e). Note endozonal (e)–exozonal (x) growth cycles, growth check at former frond margin (large arrow), absence of median lamina within endozonal region and lack of cystiphragms within recumbent zooecia. Long.–Transv., MSU 220314-00253, Eden Shale, Indiana, × 13.

always discontinuous; they are separated by exozonal growth in the parent frond and thin-walled growth at the bases of secondary fronds.

The rounded to elliptical, optically hyaline tubes described by Boardman and Utgaard (1966), and herein termed median styles, display an ultrastructure identical to that of the granular layer (text-fig. 3). The median styles are composed of tightly interlocking granules with an ultrastructure identical to that of the median granular layer. Like acanthostyles and the median rods of ptilodictyines (Karklins 1983), they were not hollow tubes, but continuously deposited, solid structures. Similar structures occur in the mesotheca of the trepostome *P. perforata* Nekhoroshev (Volkova 1974). In *Peronopora* they are generally centered on the junctions between adjacent zooecial ranges and extend the length of one to several zooecial bases in longitudinal section. Oblique sections through the mesostyles could produce the 'mesothecal lenses' (Pl. 79, figs. 3 and 4) described by Tavener-Smith and Williams (1972). Where mesostyles occur within the granular layer, they may be undifferentiated from it or separated by a thin parting. Median styles may occur in the absence of the medial granular layer.

EXPLANATION OF PLATE 79

Fig. 1. *Peronopora vera*. Fine ultrastructure of median granular layer. Fractured section, Transv., MSU 220335-00241, × 1,000.

Figs. 2–6. *P. decipiens*, MSU 220314-00415, Dillsboro Fm., Indiana. 2, Growth check in median lamina showing outer laminar layer (OLL) folded around distal tip of median granular layer (MGL). Long., × 720. 3, lensoidal region (median style (MS)) of median granular layer (MGL) between compound zooecial walls (ZW). Outermost laminae of outer laminar layer (OLL) continuous with recumbent zooecial wall (centre, top, and bottom). Transv., × 940. 4, elliptical median style. Zooecial wall at top right. Labelled as above. Long., × 1,300. 5, median lamina; pluricupular crystallites of outer laminar layer (OLL) and median granular layer (MGL). Transv., × 3,200. 6, median lamina. No medial parting present. Note thinning of median granular layer at right. Labelled as above. Transv., × 660.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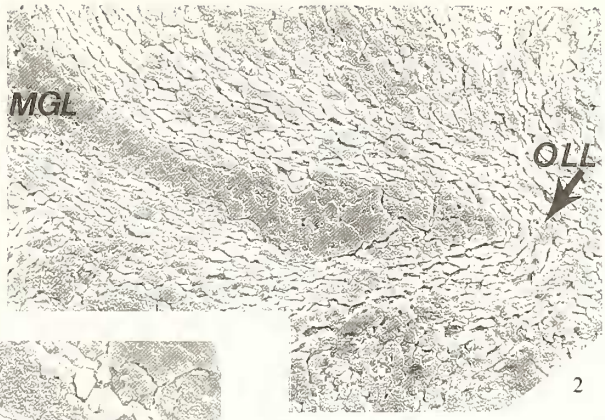

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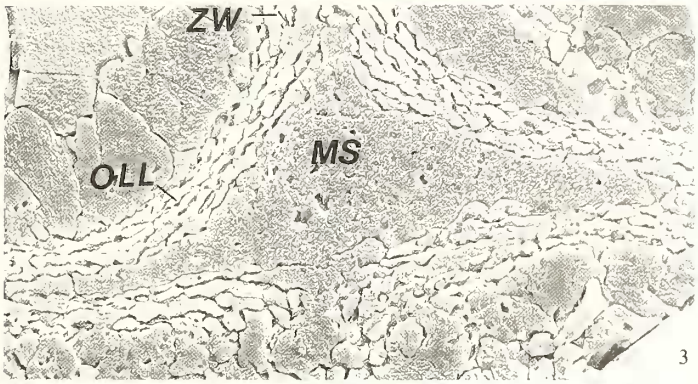

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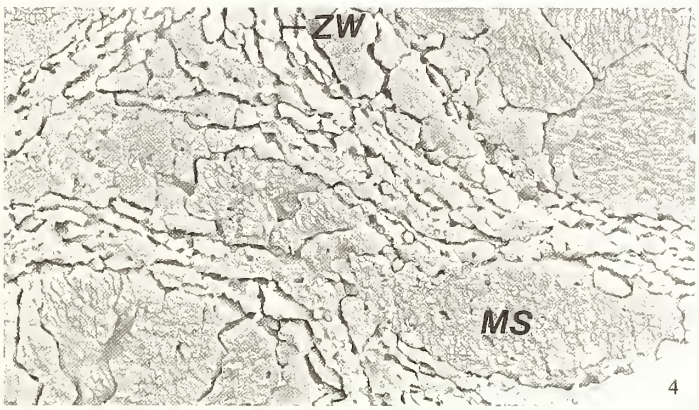

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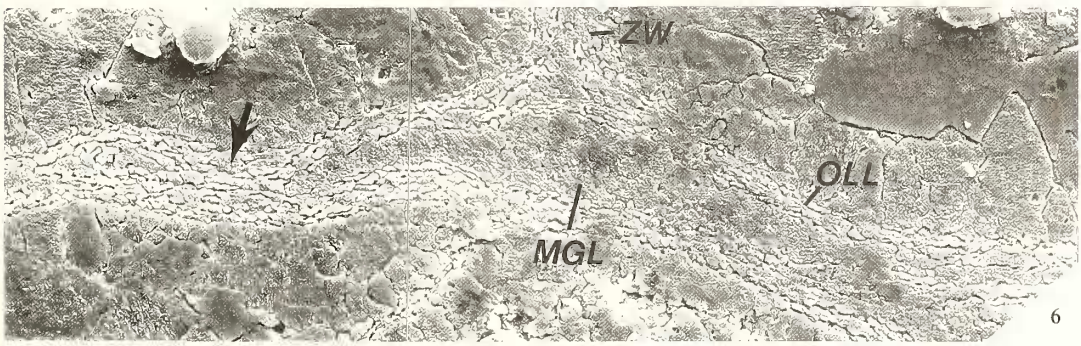

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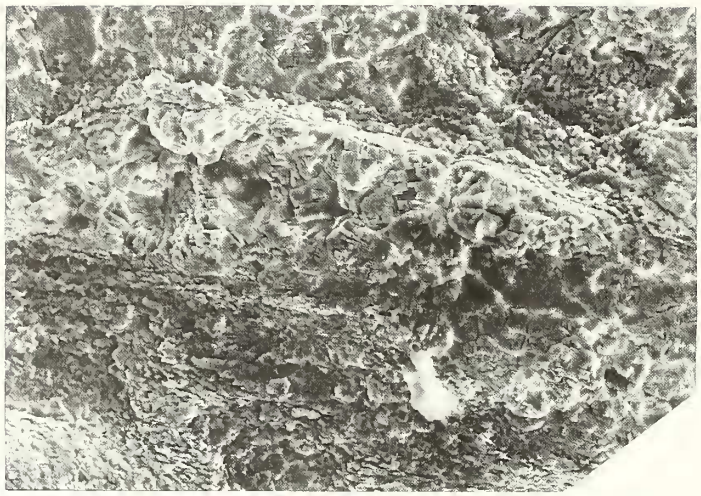
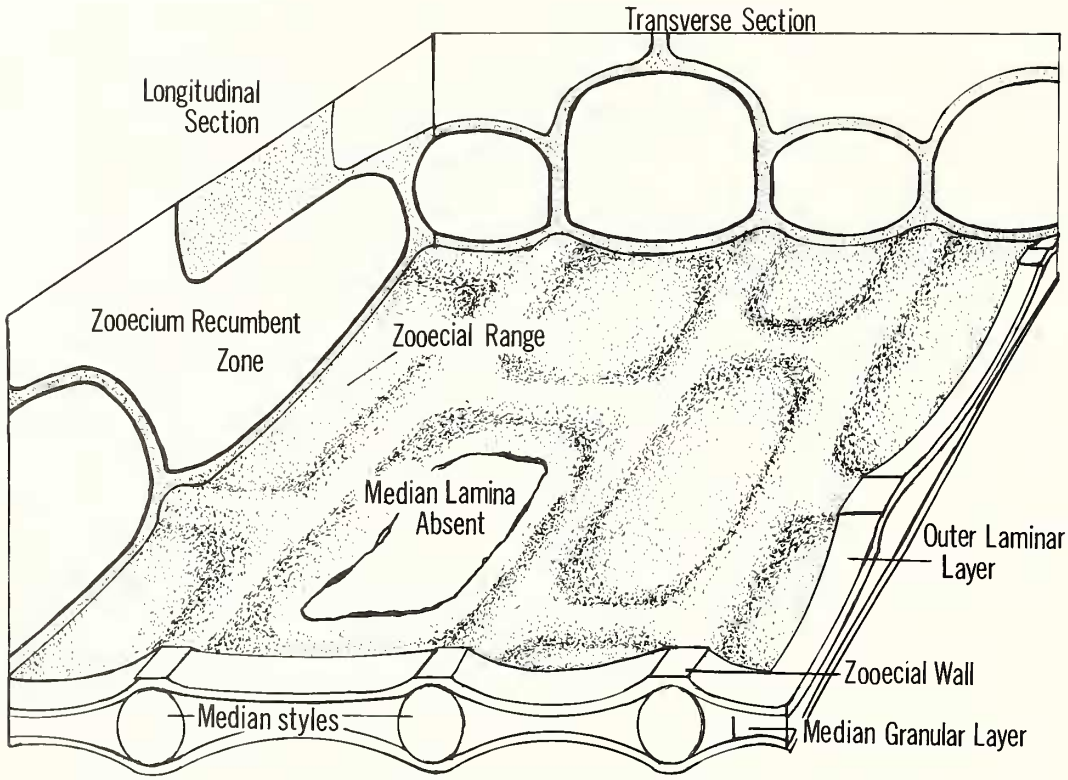
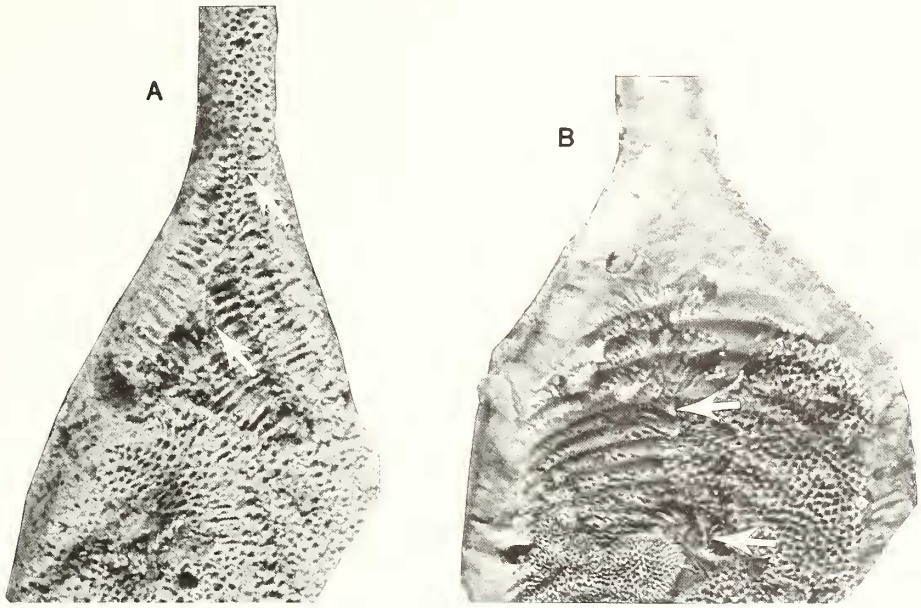


TEXT-FIG. 3. *Peronopora vera*, fine ultrastructure of median style. Fractured section, Transv., MSU 220335-00241, ×200.



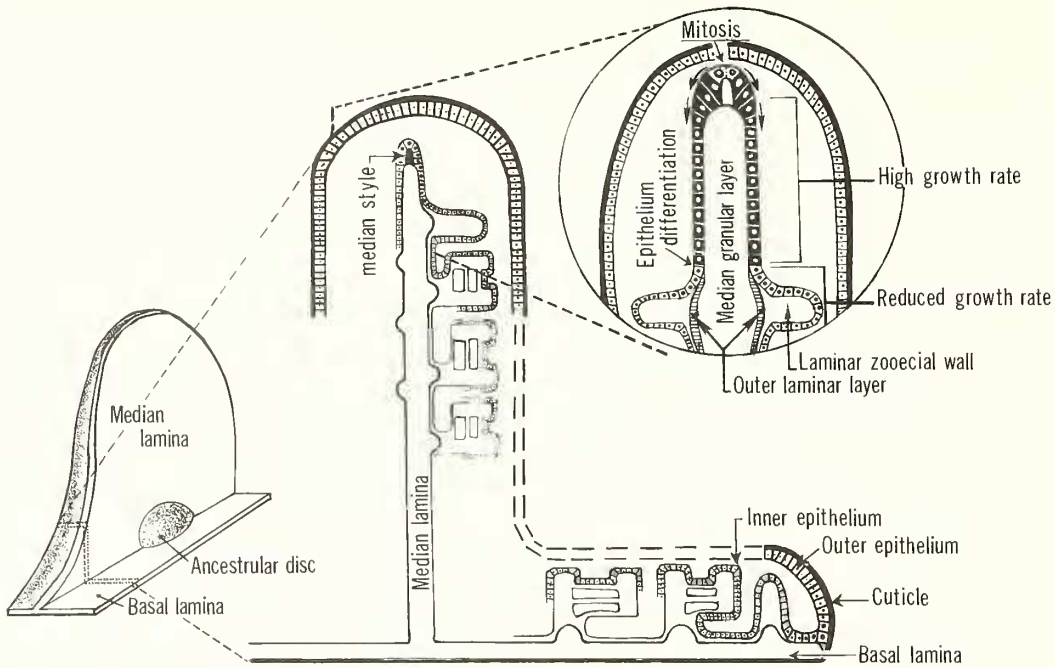
TEXT-FIG. 4. Reconstruction of the median lamina showing distribution of median styles, lensoidal swellings, and local thinning of medial granular layer.

The distribution of mesostyles and thickness variation within the median lamina suggest that the mesostyles and lensoidal regions served as space-filling structural supports between adjacent zooecia (Pl. 78, fig. 9). Tavener-Smith (1969*b*) suggested that median rods in fenestellids may have served to anchor the median lamina skeleton to the outer epithelium or cuticle. The median styles of *Peronopora* could have assumed a similar function, although evidence indicates (see below) that they were secreted by inner, not outer epithelium, and thus not directly associated with outer epithelium or cuticle. Short discontinuities of the median layer may represent local thinning or non-deposition of the median granular layer beneath recumbent zooecial bases rather than an actual discontinuity of the skeletal layer. A three-dimensional reconstruction of the median lamina is illustrated in text-figure 4.



TEXT-FIG. 5. A, *Peronopora decipiens*, colony base showing median lamina (arrows), basal lamina not preserved, MSU 220314-00415, ×5. B, *P. decipiens*, colony base showing junction of median lamina (arrows) and basal lamina. Latter not preserved, but presence indicated by epizoans underlying (on opposite side of) preserved ornamentation of bivalve, upper surface of which was encrusted by young *Peronopora*, MSU 220314-00486, Dillsboro Fm., Indiana, ×5.

An understanding of the skeletal growth of *Peronopora* depends on the relationship between the exterior-walled basal lamina, median lamina, and interior-walled skeleton (Tavener-Smith and Williams 1972). Complete basal portions of early colonies demonstrate that the median lamina was continuous with the basal lamina of the primary frond (text-fig. 5). The median lamina arose after the formation of an elliptical ancestrular disc (Hickey, in press). Completion of the disc was followed by reorientation of the zooecia at the proximal and distal margins of the disc so that the normally basal portions of adjacent zooecial tubes became lateral walls separating oppositely diverging zooecia. The median lamina was formed by vertical extension of the basal lamina following the completion of the recumbent zones of these zooecia. Thus the median lamina was generated at the terminal margins of the primary frond and arched over the ancestrular disc with continued vertical frond growth. Text-figure 6 illustrates the primary features of early astogeny and relationships among the major skeletal structures in bifoliate *Peronopora*.



TEXT-FIG. 6. Growth model for bilaminate species of bifoliate *Peronopora*. *Left*, reconstruction of relations between median and basal laminae and ancestrular disc; *Centre*, relationships between epithelial layers and skeletal layers, median lamina and basal lamina; *Right*, detail of growth model showing region of epithelial differentiation for high and reduced growth rates, granular and laminar skeleton.

Continuity of the median and basal laminae implies, but does not require, deposition in contact with the cuticle. A tendency for fractured specimens to split along separate linear series of zooecia or lamina could be taken as evidence of deposition against a cuticle (Sandberg 1977). Although zoaria of *Peronopora* readily split along the median lamina, the parting tends to be irregular; it usually passes along alternate sides of the central layer rather than through its centre. The inner surface of the median lamina does not exhibit an ultrastructure comparable to the planar spherulitic crystallites of fixed-walled skeleton in cheilostomes (Sandberg 1983).

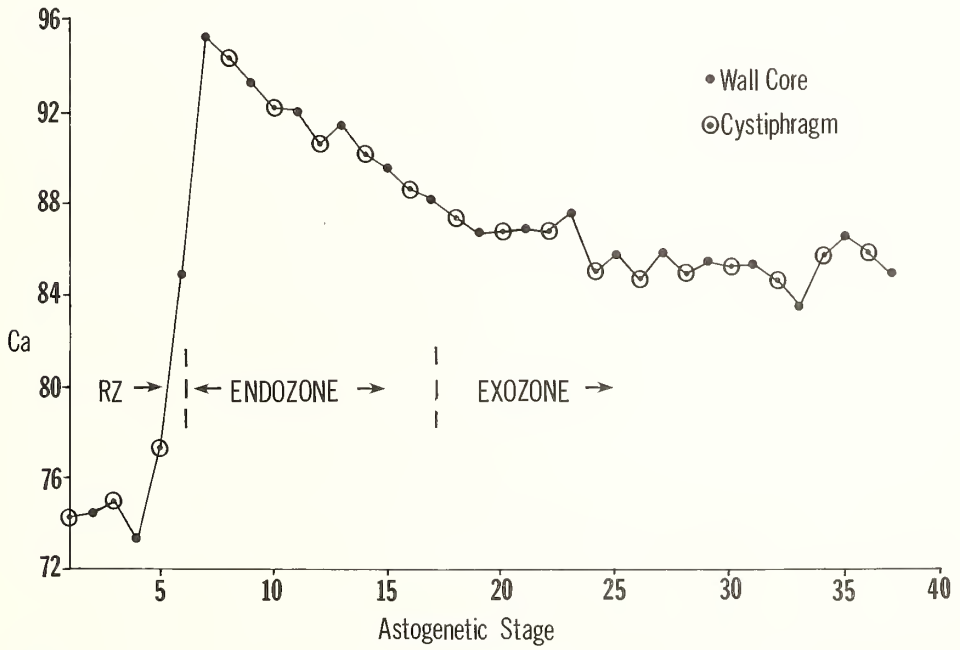
Tavener-Smith and Williams (1972) concluded that the median lamina of *P. milleri* was not deposited against a cuticle because the median lamina consisted of discontinuous 'mesothecal lenses' with no evidence of a medial parting. This study found no ultrastructural evidence of a medial parting within the continuous medial layer (Pl. 78, fig. 9; Pl. 79, figs. 5 and 6) despite the common occurrence of a dark medial line in thin section. Folding of laminar internal-walled skeleton around the distal ends of median granular layer 'segments' (Pl. 79, fig. 2) indicates that a secretory epithelium of the median lamina could not have been located between the median granular layer and the outer laminar layer as suggested by Tavener-Smith and Williams (1972). The discontinuity of the median laminae of primary and secondary fronds of *Peronopora* also shows that median lamina skeleton could not have been deposited against cuticle or within a fold of (basal) epithelium. Thus, the median lamina was continuous with the upper portion of the basal lamina but must have been deposited by inner epithelium at the growing margin of the colony (text-fig. 6). The inner epithelium appears to have been capable of secreting skeleton which was ultrastructurally very similar or identical to exterior-walled skeleton (see discussion).

ELEMENTAL COMPOSITION

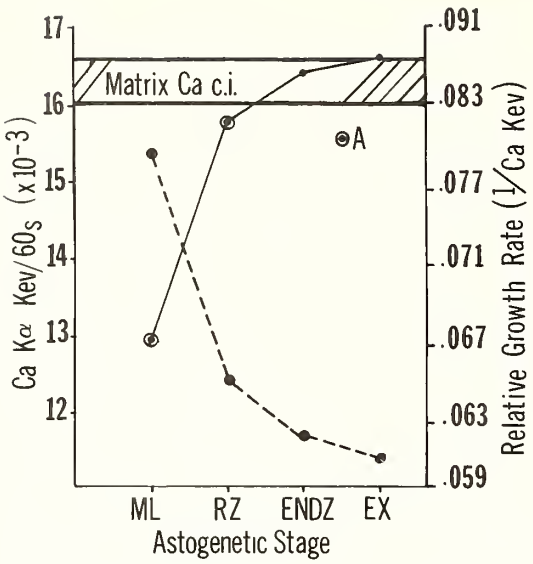
Elemental rhythms and ontogenetic trends

Elemental abundances in some organisms other than bryozoans are known to vary with tidal (Rosenberg and Jones 1975), diurnal (Schmalz and Swanson 1969), or seasonal cycles (Bryan 1973; Goreau 1977; Crisp 1975). If the physiological process of skeletal growth do interact with ambient levels of trace elements in the environment, or if non-equilibrium modifications in elemental composition occurred in conjunction with the periodic formation of structures, such processes could be evinced in abundance cyclicities. Cystiphragms are periodically formed structures which could have been deposited in association with tidal cycles (Bartley and Anstey 1983). A single zooecial wall of *P. vera* was analysed for periodic abundance fluctuations of Ca, Cu, Si, Fe, Mg, Mn, and Nb between the laminae of cystiphragms and intervening regions of laminar zooecial wall deposited between cystiphragms. This analysis was designed to determine whether elemental abundances were distributed in a systematic manner in association with the periodic emplacement of cystiphragms. With the possible exception of Ca, none of the elements displayed periodic structural variations.

There is some indication of a periodic fluctuation of Ca within the endozones and exozones of the autozooecial wall. Ca abundance changed in a systematic manner with ontogeny (text-fig. 7). Minimal values in the thin-walled recumbent zone increased abruptly during transition from the recumbent zone to the lower endozone. Abundance gradually decreased from the endozone through the latest exozone. Within the exozone, Ca levels of cystiphragms and contiguous zooecial wall laminae are generally lower than those of intervening laminae of axial positions in the wall, but the difference is not statistically significant. This structural fluctuation is also present, though weakly developed, within the endozone.



TEXT-FIG. 7. Distribution of Ca in zooecial wall of *Peronopora vera*. MSU 220335-00252. RZ = recumbent zone. 'Astogenetic Stage' approximated by datum points located at equal intervals, alternately within wall axis and on each successive cystiphragm wall.



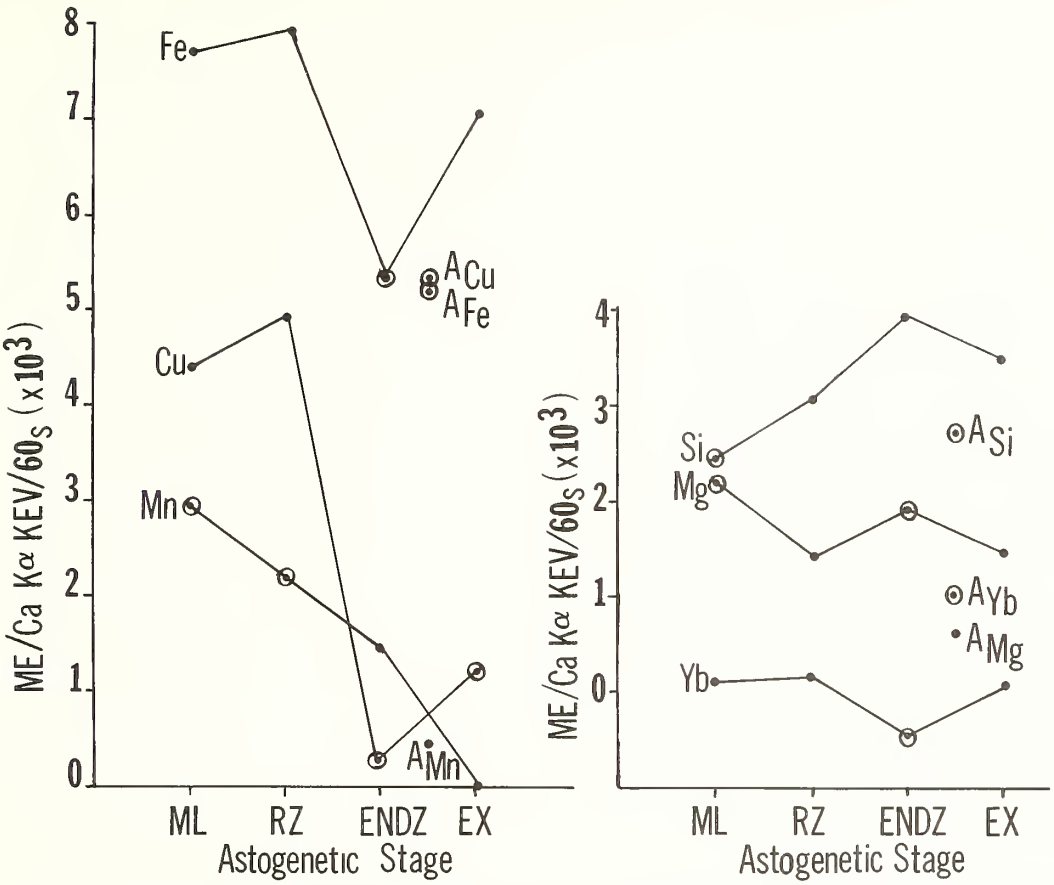
TEXT-FIG. 8. Distribution of Ca among median lamina (ML), recumbent zone (RZ), endozone (ENDZ), exozone (EX), and acanthostyles (A, circled) for fifteen zooecia of *Peronopora vera*. MSU 220335-00252. Circled datum indicates Ca density value differing significantly from void cement. C.I.= confidence interval for Ca density levels of zooecial void cement. Solid line: Ca density distribution. Dashed line: relative growth rates of astogenetic zones and skeletal structures.

Rosenberg (1980) has stressed the need for replicated analyses in studies of this kind. His review of similar studies of bivalves noted that element abundances may vary among planes of cross-section and among individuals, suggesting that allometric analyses of ontogenetic trends may explain much of the variation in compositional trends. Thus, although the above results are interesting, no general inferences should be drawn from them. In contrast, the second analysis is based on the mean values of Ca and trace element abundances from three astogenetic zones, acanthostyles, and the median lamina measured in 15 individual autozooecia of a single colony. Statistical treatment of these data permits inferences about the relationships between compositional change and growth. The difference in exozonal Ca abundance between the former and following analyses were probably due to the absence of replicate data from other zooecia and the collection of data from points of very limited surface area (small beam size) in the former.

Astogenetic trends

Analysis of fifteen zooecial walls revealed a Ca trend that is broadly similar to that of text-figure 7, but differs critically in the relative values of the endozone and exozone. Ca levels are minimal in the median lamina and become progressively greater in the recumbent zone, endozone, and exozone (text-fig. 8). All pair-wise comparisons between astogenetic zones and other structures show significant differences in Ca abundance. Ca abundance within the exozone is significantly greater than that of the endozone at $p = 0{\cdot}10$. Acanthostyle axial cores contain significantly less Ca than the recumbent zone, endozone and exozone ($p < 0{\cdot}05$), but significantly more Ca than the median lamina ($p < 0{\cdot}05$). The median lamina contains significantly less Ca than acanthostyles and astogenetic zones of zooecial wall skeleton ($p < 0{\cdot}05$).

Ca densities of the endozone and exozone do not differ significantly from that of the zooecial void cement. Thus it is possible that Ca abundance within void matrix could have varied in a proximo-distal manner similar to that of the skeleton. However, some aspects of the Ca distribution suggest that the observed trend is not a product of diagenesis. Significant differences ($p < 0{\cdot}05$) do occur among the void cement and acanthostyles, recumbent zone and median lamina. Ca concentration within void cement was measured at approximately the mid-point of each zooecial tube; a position equivalent to that of the inner exozone. Acanthostyle Ca abundance was measured within the exozone, yet is significantly lower than that of the matrix, exozonal, and endozonal wall. In addition, petrologic criteria indicate that the recumbent zone of *Peronopora* and other



TEXT-FIG. 9. Trace element distributions in *Peronopora vera*. MSU 220335-00252. Labelled as for text-fig. 8. Circled points indicate densities significantly different from void cement.

taxa is less-well calcified than endozone or exozone (Boardman and Utgaard 1966). Thus, it appears that the trend in skeletal Ca abundance is not a product of diagenesis. Additional studies of this kind are needed to confirm or reject the results of this study.

Mg abundance declined slightly over the course of astogeny in *P. vera* (text-fig. 9). Because Mg readily substitutes for Ca, it is expected to vary inversely with Ca. The overall trend is toward decreasing Mg concentration, yet Mg is most abundant within the median lamina and endozone, and least abundant in the recumbent zone and exozone. Mg concentrations of the median lamina and endozone are significantly greater than that of the void cement ($p < 0{\cdot}05$).

Mn concentration decreased monotonically with autozooecial age in *P. vera* (text-fig. 9). Mn abundance is inversely proportional to Ca density across astogenetic zones, a relationship which could reflect elemental substitution. Mn concentrations within the median lamina and recumbent zone are significantly greater than that of the void matrix ($p < 0{\cdot}05$).

Cu and Fe exhibit parallel fluctuations over the course of astogeny; both generally decline with increasing age (text-fig. 9). Fe and Cu reach maximal abundance in the recumbent zone and acanthostyles respectively. The minimum values for Fe and Cu occurred in acanthostyles and the endozone respectively. Levels of Fe in the endozone and acanthostyles are significantly less than that of the void cement. Cu abundances in the endozone and exozone are significantly lower than

that of the void cement. Cu concentration in acanthostyles is significantly greater than that of the void cement. Si gradually increased with age through the endozone but declined somewhat within the exozone. Si concentration is significantly less abundant in the median lamina than in the void cement. Yb concentration remained essentially constant with increasing age but differed significantly from the void cement in the endozone.

Structural variation

Acanthostyle cores contain significantly more Cu than the median lamina, endozone, or exozone. The concentrations of Fe, Cu, Si, and Yb in acanthostyles differ significantly from that of void cement. The median lamina contains significantly more Mn than the zooecial wall skeleton and void cement. Si and Mg concentration are also significantly greater in the median lamina than in the void cement.

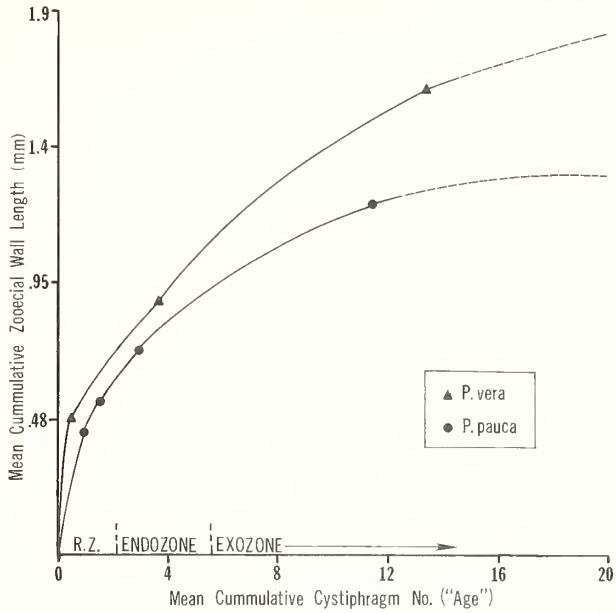
DISCUSSION

Astogenetic growth zones

Tavener-Smith (1969*a*, *b*, 1975) and others have proposed that differences in crystallite morphology reflect differences in the continuity and rates of crystallite and skeletal secretion and growth among astogenetic zones. These inferences were based on consideration of the effects of the thermodynamics of crystallite growth on ultrastructure, the differential response of skeletal structure to episodic *versus* continuous growth, and the astogenetic succession of crystallite/skeletal wall morphologies. These hypotheses of growth rate are important for two reasons. Firstly, they can increase our understanding of growth, development, and skeletal formation. Secondly, knowledge of the relative growth rates of skeletal structures can be used to explain the evolution of zooecial wall and other skeletal structures. The results of elemental analyses (particularly Ca) in *Peronopora* support the inferred associations between crystallite/skeletal morphology and secretion rates. The data also support inferences about the relative rates of growth among astogenetic zones.

If it can be assumed that EDS measurements of Ca abundance reflect the density distribution of calcium within the skeleton (and that this distribution is not a result of diagenesis), relative levels of Ca can be used as a gauge of relative growth rates. It is assumed that the relative abundance values obtained from a given surface area can be extrapolated to proportional values of density when comparing surfaces of approximately equal area. Rosenberg (1983) argued that this assumption was a valid interpretation of the distribution of Ca in fossil brachiopods. This interpretation is based on the thermodynamics of crystal growth which predict an inverse relationship between growth rate and Ca density. Thus zones of continuous and rapid growth should display lower Ca densities than zones of slower, laminar (episodic) growth. An equivalent relationship should exist among Ca densities and astogenetic zones of predominately laminar growth. Less 'densely' laminated recumbent zone and endozone should display lower Ca densities than thicker-walled exozone. In addition, granular and irregular crystallites should contain less Ca than laminar skeleton and tabular crystallites. A corollary of this relationship predicts that trace elements which commonly substitute for Ca should be greater within skeleton with lower Ca densities and by inference, higher rates of crystallite secretion and skeletal growth. Those which easily complex with organic materials could be expected to be more common in more densely laminated wall and/or zones of disordered growth in wall axes.

The thin-walled recumbent zone and endozone are commonly believed to have been faster growing than the thick-walled exozone. The relative densities of Ca in these astogenetic zones are in accord with theoretical predictions of Ca density behaviour with growth rate variation (text-fig. 4). These data also support the petrologic evidence that autozooecial recumbent zones in *Peronopora* were lightly calcified (Boardman and Utgaard 1966). Therefore Ca density data support the hypothesis that growth rate decreased exponentially with increasing age from the recumbent zone through the exozone in *Peronopora*. The recumbent zone formed more rapidly than the endozone



TEXT-FIG. 10. Growth curves based on cystiphragm distribution per unit wall length for *Peronopora vera* (MSU 220314-00508, Eden Shale, Indiana) and *P. pauca* (paratype, IU8252G 160-1170, Indiana University specimen, Whitewater Fm., Indiana).

and the endozone formed more rapidly than the exozone. The results also allow inferences about the relative growth rates of other structures. The median lamina was secreted most rapidly, followed by acanthostyle cores and the recumbent zone. Granular crystallites of optically hyaline skeleton generally reflect higher rates of secretion and growth than tabular crystallites within internal-walled skeleton. Presumably, these results could be extrapolated to other taxa which show various modes of skeletal differentiation within and among recumbent/endo- or exozones, mesothecal, and exterior-walled skeleton. Further EDS analyses on other taxa should provide interesting data on bryozoan growth rates.

If rates of wall growth gradually decrease from the recumbent zone through the exozone, and if cystiphragms or other intrazooecial structures were formed with a regular periodicity (Bartley and Anstey 1983) then it is possible to construct growth curves for bryozoans. The area subtended by cystiphragms and the spacing between cystiphragms decreases (degree of cystiphragm overlap increases) from the recumbent zone through the endozone in bifoliate *Peronopora* (Hickey, in press). Spacing is minimal and appears to remain relatively constant throughout the exozone. The size/spacing distributions are consistent with the assumption that cystiphragms were formed with a regular periodicity while growth rates of zooecial wall decreased with age. Thus, a plot of the cumulative number of cystiphragms per unit length of zooecial wall should reveal changing rates of wall growth. Text-figure 10 illustrates preliminary results of such growth curves for single colonies of *P. vera* and *P. pauca*. That these growth curves are of the same shape as that of the Ca density data (and the inverse of the Ca growth rate curves) lends support to the hypotheses that zooecial wall growth rates generally decreased with increasing age. Knowledge of the actual time lapse (e.g. fortnightly cycles, etc.) between cystiphragm formation is not necessary for such a reconstruction of relative growth rates. The growth curves for *P. pauca* and *P. vera* suggest that the growth rate of the former species declined more rapidly than that of the latter; a conclusion consistent with the thicker exozonal walls of the former species. The ability to construct relative growth curves could add to the understanding of the palaeobiology and systematics of bryozoans. Such growth curves could be used as taxonomic descriptors.

Trace element data may also have a bearing on interpretations of skeletal growth rates. Several studies have found that Mg and Mn concentrations can vary with growth rate. Goreau (1977)

found an increase in Mg with decreasing growth rate in the coral *Montastrea annularis*. However, Zolotarev (1974) documented a decline in Mg with reduced growth rate in the bivalve *Mytilus yessoensis*. A gradual increase with age and reduced growth rate is evident in the data of Moberly (1968) for the bivalve *Aequipecten irradians*. Crisp (1983) reported a decreasing Mn concentration with increasing age in freshwater bivalves. However, he also found that Mn concentrations were greatest in the slowest growing portions of the oldest growth increments. Crisp (1975) found an apparent habitat dependence in Mn ontogenetic trends; Mn decreased with increasing age among individuals of the bivalve *Lampsilis* sp. from one habitat, but increased with age among individuals from a different habitat. The bivalve *Anodonta corpulenta* displayed an increase in Mn with increasing age.

The monotonic decrease of Mn density with increasing age in *Peronopora* is consistent with the expected distribution of trace elements with respect to Ca and inferred growth rates (text-fig. 9). The Mn trend could reflect a direct physiological function of skeletal growth rates and/or a function of elemental substitution for Ca. Substitution is expected to have been greater in faster growing zones of lesser Ca density such as the median lamina and recumbent zone. However, simple substitution is probably an inadequate explanation for the Mn trend given that the incorporation of Mn in cheilostome skeletons is under physiological control (Sakagami *et al.* 1984). Mg also shows a slight decrease in density with increasing age and decreasing growth rate; however, these data are much less definitive. Mg concentration is expected to have been a simple equilibrium function of crystallite growth rate (Sakagami *et al.* 1984).

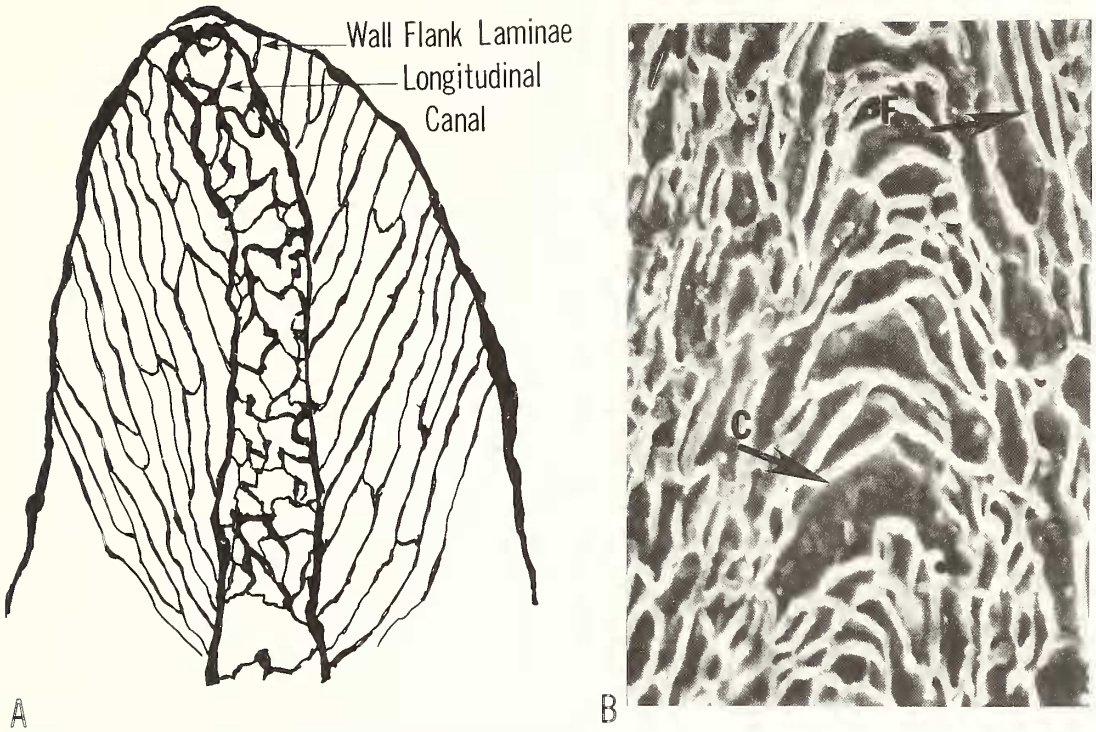
The meaning of the astogenetic trends of other trace elements is not entirely clear. Each of the elements analyzed show significant density differences between one or more astogenetic zones and the void cement. Some of the variation could be attributed to substitution for Ca and thus, could be interpreted as rate related phenomena. The data suggest that some elements could have been preferentially concentrated/excluded at various stages of growth or among skeletal structures. By analogy with the composition of cheilostomes (Sakagami *et al.* 1984), the abundances of Fe, Cu, and Mn could represent products of differential concentration or exclusion through physiological control over ambient levels. Alternatively, the data could indicate that astogenetic stages and skeletal structures were differentially influenced by diagenesis as a function of crystallite type and/or ultrastructural variation within laminated zooecial wall. Additional studies could conceivably determine whether such results reflect ontogenetic variation, differential response to diagenesis, or the influence of environmental factors.

The differences in Ca density among growth zones of laminar skeleton, crystallite types and skeletal structures in *P. vera* are consistent with independent inferences about relative rates of skeletal growth based on observations of microstructural variation in this and other studies. Such compositional variations appear to reflect real differences in the physiology of skeletal growth. The distributions of most trace elements are not as easily interpreted as is that of Ca. However, the distributions of Ca, Cu, and Mn among crystallite types are generally consistent with predictions of thermodynamics and a variety of qualitative observations and may be extended to skeletal growth rates during astogeny.

Zooecial wall growth

Tavener-Smith and Williams (1972) suggested that differences between thicknesses of the laminae of wall axes and flanks within some 'amalgamate' trepostomes are due primarily to oblique orientations of laminae within the axial zones. The 'bimodal' nature of axial crystallite dimensions and lamina frequencies in *Peronopora* produce indistinct zones of laminae which resemble the independent wall units discussed by Boardman (1960). These zonal microstructural variations indicate that axial crystallite shape and thickness differences are not entirely artefacts of lamina orientation. Zonal differences in crystallite morphology and lamina number could be characteristic of taxa with cyclical growth rates.

Some aspects of the central wall structure of the Recent tubuliporate *Heteropora pelliculata* Waters (Ross 1976, 1977) provide a developmental analogue for interpretation of differential wall



TEXT-FIG. 11. A, zooecial wall structure of *Heteropora pelliculata*, decalcified long. sec. Redrawn from photograph in Ross (1976). B, *Peronopora vera*, exozonal autozooecial wall. Disordered central wall structure (C), laminar wall flanks (F). Acetate peel, Long., MSU 220335-00239, Eden Shale, Ohio, ×3,000.

flank/axis ultrastructure in *Peronopora* and similar trepostomes. Distal portions of zooecial walls of *H. pelliculata* display irregularly shaped, disordered crystallites in a relatively dense organic matrix within central longitudinal 'canals' (Ross 1976, text-fig. 1). Ross (1977) suggested that the 'canals' may serve as loci for locally accelerated growth and conduits for the resorption and distribution of skeletal and other materials. Acetate peels (negative replicas) of the axial zone of zooecial walls in *Peronopora* bear a striking textural resemblance to the distribution of the organic matrix in the interior of the longitudinal canals of decalcified specimens of *H. pelliculata* (compare text-fig. 11*a*, *b*). It is not suggested that the axial zones in *Peronopora* contained longitudinal 'canals' as Ross proposed for *H. pelliculata* and it should also be noted that the zooecial wall flanks of *H. pelliculata* are proximally oriented, unlike those of *Peronopora*. However, the textural similarity between the axial zones of the two taxa strongly suggests that the axial zones of *Peronopora* could have been characterized by relatively rapid, disordered crystallite growth and higher organic content similar to *H. pelliculata*. The dynamics of crystallite growth in general suggest that irregularly shaped, disordered crystallites were more rapidly formed than those with uniform shapes (Tavener-Smith 1969*b*). This interpretation is supported by Ca data which indicates that the similar granular crystallite morphologies of the median lamina and acanthostyle cores were a product of increased rates of crystallite secretion.

Large, granular crystallites also occur between the laminar annular thickenings (monilae) of *Stenopora crinita* (Armstrong 1970) and the laminar monilae of *Tabulipora* Young. Evidence of fortnightly tidal cycles has been found within the monilae of *Tabulipora* (Rabbio and Regalbuto 1985). Constricted zones of granular zooecial wall occur between the fortnightly cycles recorded within the monilae of *Tabulipora*. The limited width and granular morphology of the constricted

regions suggests that these portions of the wall were formed more rapidly than the laminar monilae. Thus wall growth in *Tabulipora* appear to have varied between slow, laminar (episodic) and rapid, continuous modes in conjunction with tidal cycles.

Microstructural zonation of the crystallite morphology of *Peronopora* is inferred to reflect periodic variations in growth rates and episodicity of laminae formation. Although most individual laminae are difficult to trace for long distances within a wall, the number of laminae intersected by a line drawn parallel to the zooecial wall growth axis can provide rough estimates of laminae frequency. Counts of laminae within a given unit wall length made by independent observers differ significantly from the null hypothesis of no difference in means. However, differences in laminae frequency between axial and flank regions within a given unit length differ significantly ($p < 0{\cdot}05$) despite the variation attributable to observational error. Lamina frequency consistently differ by a factor of two or more between zooecial wall flanks (mean = 19·3) and axes (mean = 27·4) per unit (distal) length. In addition, laminae appear to be at least twice as numerous—per unit wall length—within the laminar zones of wall axes than within zones of irregular axial crystallites. Axial laminae within intervening zones of larger, irregular crystallites are often less distinct than those of wall flanks and laminar zones of the axis. These frequency distributions of laminae reflect a greater degree of intercalation between the laterally discontinuous laminae of axial zones than among laminae in the adjacent wall flank, and an alternation between laminar and irregular crystallite growth within the wall axis. It is inferred that the episodicity of laminae formation was greater (and rate of skeletal formation thus lower) within laminar portions of axial zones than on wall flanks. Irregular crystallite morphology can be attributed to increased rates of crystallite secretion and decreased episodicity by inference from the similarity between irregular and granular crystallite ultrastructures.

The irregular and disordered crystallite morphology and approximate doubling of laminae number within different zones of the zooecial wall axis of *Peronopora* strongly suggests periodic variation of growth rate and episodicity within the axis. Structural differences between wall axes and flanks suggest periodic alternations between increased growth rates and increased episodicity, respectively. Structural zonation is most pronounced within mesozooecial walls. Zones of irregular crystallites within the axial wall occurring proximal to cystiphragm/tabula emplacements could indicate increased rates of crystallite secretion preceding cystiphragm/tabula formation. The increased frequencies of laminae composed of more tabular-shaped crystallites occur in zones which are contiguous with cystiphragm and tabula walls. This structural variation suggests slower rates of crystallite secretion and increased episodicity of lamina formation during periods of cystiphragm formation.

Periodic variation in ultrastructure could be linked to periodicities of element abundances. Rosenberg and Jones (1975) found regular fluctuations in Ca and S abundance in living specimens of the bivalve *Cardium edule* which were correlated with tidal cycles. Individual lamina of bryozoan skeletal walls are presumed to be daily deposits (Tavener-Smith 1969*b*; Rabbio and Regalbuto 1985). Laminae are nested within periodic cystiphragm emplacements; events of a higher temporal order that could be linked with tidal cycles (Bartley and Anstey 1983). Variation in Ca density could be expected in association with the structural variation of zooecial wall which occurred during the cystiphragm formation cycle in *P. vera*. The observed variation of Ca density between periods of cystiphragm emplacements and normal wall growth in *P. vera* could reflect cyclic growth phenomena associated with periodic changes in environmental variables (text-fig. 7). However, the data are equivocal because the difference between mean Ca levels in cystiphragms and zooecial walls is not statistically significant. The results do indicate that further studies of relationships between structural periodicities, Ca variations and growth rhythms are warranted.

Evolution of wall structure

If crystallite morphologies and astogenetic zones of growth can be linked to differential growth rates, the evolution of wall structure among closely related taxa may be described in terms of heterochronic change. Tavener-Smith (1969*a*) and Brood (1976) have noted the presence of short

distal extensions of granular exterior-walled skeleton at the base of zooecial walls in free-walled taxa. Larwood and Taylor (1979) proposed that the evolution of free-walled taxa from primitive fixed-walled taxa in the Palaeozoic could be interpreted in terms of paedomorphic heterochronic changes which prevented the coalescence of free-walled skeleton with outer epithelium. The early termination and/or reduced growth rate of the granular external-walls could have been the principal heterochronic change leading to the origin of paedomorphic free-walled taxa. This interpretation of skeletal growth rates supports the hypothesis of Larwood and Taylor (1979). Given either early termination (progenesis) or reduced growth rate (neoteny), the phylogenetic phenomenon would have been reverse recapitulation (terminology of Alberch *et al.* 1979).

Tavener-Smith and Williams (1972) noted that the optical differences between the zooecial wall microstructures of the former trepostome suborders Amalgamata and Integrata reflect the increased 'granularity' (irregularity) and greater dimensions of axial wall crystallites in the latter. These suborders may have grouped together taxa with homogeneous rates of laminar growth, and taxa with locally accelerated rates of axial growth, respectively. Given a hypothetical ancestral taxon with homogeneously laminar growth, accelerated axial growth in a derived taxon could be interpreted as a peramorphic product representing acceleration. The evolution of the 'amalgamate' Atactotoechidae from the 'integrate' Amplexoporidae (Astrova 1965, p. 114) provides a concrete example. In this case, the derivation of uniformly laminar walls from primitive granular walls could be viewed as an example of paedomorphosis representing the process of neoteny in a phylogenetic pattern of reverse recapitulation.

The evolution of wall structure among *Peronopora*, *Prasopora*, and *Atactoporella* has been interpreted in terms of heterochronic processes (Hickey, in press). *Prasopora* can be considered primitive and probably ancestral to *Atactoporella* (Astrova 1978) and *Atactoporella* appears to be the ancestral sister group of *Peronopora* (Hickey, in press). *Prasopora* is characterized by a 'granular' zooecial wall structure, while zooecia of *Atactoporella* and *Peronopora* have predominately laminar walls. The derived laminar wall structures of the latter two genera appear to have evolved through a paedomorphic decrease in the rate of wall growth during astogeny.

Acanthostyle development and evolution

The epithelial origins of acanthostyles are uncertain. The optically hyaline appearance of the axial cores of trepostome acanthostyles and portions of 'heterostyles' (Blake 1983) resembles that of exterior-walled skeleton. This suggests that the axial crystallites of trepostome acanthostyles could have been secreted by outer epithelium as Tavener-Smith (1969*b*) proposed for fenestellid skeletal rods and 'primary skeleton'. However, secretion of core crystallites by outer epithelium in trepostomes appears to be precluded by the lack of any examples in which acanthostyle cores are proximally continuous with exterior-walled skeleton. Overgrowth of the axial core terminus by laminar skeleton in the trepostome *Leptotrypella? praecox* Boardman (Boardman 1983, text-fig. 51-1*c*, p. 104), the complex growth mechanics needed to explain the alternation of hyaline and laminar skeleton in trepostome 'heterostyles' (Boardman 1983, p. 105), and the different ultrastructures of acanthostyles and median lamina in *Peronopora* also argue against secretion of axial core skeleton by outer epithelium. Yet, the microstructural contrasts between axial cores and sheath laminae indicate there were distinct growth differences of some kind.

Armstrong (1970) postulated that acanthostyle axial cores in *Stenopora* could have been deposited by patches of specialized epithelium. This hypothesis is supported by four lines of evidence in *Peronopora* as well: 1, the distinct boundary between cores and sheath laminae; 2, the contrasting morphologies of core and sheath crystallites; 3, laminar versus continuous growth modes; and, 4, differential Ca and trace element concentrations between acanthostyle core crystallites and laminar exozonal skeleton.

Several observations provide clues for an explanation of these microstructural differences. The solid nature of acanthostyle axial cores has been well established (Armstrong 1970; Blake 1973, 1983; Boardman 1983; Tavener-Smith 1969*a*). Infrequent lamination of the axial core skeleton in most taxa indicates that the deposition of granular crystallites was relatively continuous. The

topographic prominence of acanthostyles and the relationship between axial cores and sheath laminae indicate that granular crystallite deposition within axial cores was locally accelerated relative to laminae formation (Tavener-Smith 1969*a*, *b*). Occasional preservation of 'brown bodies' and pyrite grains within acanthostyle axial cores (Boardman 1983) suggests a high organic content; organic material could presumably have been more readily incorporated within core skeleton if growth were rapid. Thus axial core ultrastructure appears to be a product of accelerated crystallite secretion.

Armstrong (1970, p. 584) found iron carbonate minerals in the acanthostyles of *Stenopora*. This was interpreted as an additional indication of a specialized epithelial origin for acanthostyles. The results of this investigation can be interpreted in a similar manner. Ca densities are lower, and by inference, growth rates were higher in acanthostyles than within endozone and exozone (text-fig. 8). Substitutional elements such as Cu, Fe, and Mn are generally most abundant in acanthostyle cores (text-fig. 9). Acanthostyles are enriched in Cu, Fe, Si, and Yb relative to the zooecial void cement. High Cu levels in acanthostyle cores satisfy the predicted increase in substitutional element abundances within zones and structures with low Ca densities. The high levels of Cu are consistent with non-equilibrium skeletal formation (Sakagami *et al.* 1984). These data support the hypothesis that paurostyle cores were secreted more rapidly than endozonal and exozonal laminar skeleton. Furthermore, they suggest a more specific explanation for the skeletal differences between acanthostyle cores and laminar skeleton.

Paurostyle morphology could be explained by development of an extreme differentiation of laminar and granular crystallite growth modes. This differentiation could have been accomplished by patches of inner epithelium with particularly high rates of crystallite secretion. The disordered axial growth and irregular crystallites typical of zooecial walls in 'integrate' taxa could be considered a developmental analogue with the early stages of acanthostyle evolution in trepostomes. Paurostyles could have evolved from laminar zooecial wall by a highly localized acceleration of crystallite secretion rates. Irregular crystallites of zooecial wall axes could be invoked as a transitional step in this hypothetical transformation series.

Given the above model of acanthostyle origins, it is possible to describe the evolution of different acanthostyle types among closely related taxa in terms of heterochronic changes in rates of skeletal growth. Paurostyle morphology is assumed to be the primitive state (Tavener-Smith 1969*b*). Heterostyles, and heterostyle-like structures of some trepostomes, are composed of alternating layers of hyaline and laminar skeleton (Blake 1983). Most rhabdomesid aktinotostyles are composed of distally (and laterally) deflected laminar skeleton (Blake 1983). Aktinotostyles could have been derived from paurostyles by a decreased rate of crystallite secretion coupled with an increase in lamination episodicity. Similarly, heterostyle structure could be explained in terms of periodic alternation between the primitive paurostyle growth mode and decreased secretion rates coupled with increased episodicity. Thus both aktinotostyles and heterostyles (in part) could be considered paedomorphic products of neoteny. In this model, heterostyle evolution must have involved temporal signals which induced switching from one growth mode to another. The presumed ease with which such heterochronic modifications could occur suggests that homoplasic evolution of all acanthostyle types may have been common.

The median lamina

The median lamina arose as a distal extension of basal lamina skeleton. However, there is no evidence to indicate that the median granular layer was deposited against cuticle or within a distally directed fold of basal epithelium. The absence of a medial parting argues against the first interpretation. The second interpretation is precluded by occasional growth checks in the median granular layer which were followed by deposition of the outer laminar layer around the distal margin of the median layer, and the fact that the median granular layers of primary and secondary fronds are discontinuous. These factors, in concert with a very low Ca density indicate that the skeletal structure of the median granular layer was a product of very high, relatively continuous, rates of crystallite secretion by inner epithelium at the distal margins of the colony (text-figs. 6–

8). The generally high levels of Fe, Mn, and Cu within the median lamina (text-fig. 9) satisfy the predicted increase in substitutional element abundances and/or the presence of non-equilibrium growth products within zones and structures with low Ca densities. The similarity between granular median and basal lamina skeleton suggest that granular exterior-walled skeleton also grew more rapidly than laminar interior-walled skeleton.

The ultrastructural character of basal lamina skeleton does not appear to have been a consequence of deposition against cuticle *per se*, but rather differentiation of the crystallite secretion rates of inner epithelium (text-fig. 6). Because both granular median lamina and laminar zooecial wall skeleton are products of secretion by inner epithelium, some mechanism for differentiation of cellular processes and skeletal products is required. It is evident from the astogenetic succession of skeletal types and their common epithelial origin that new epithelial cells must have been added at the colony margin in a manner similar to the 'conveyor-belt' model of skeletal formation proposed by Tavener-Smith (1969*b*). Thus, it could be hypothesized that the stimulus for the developmental differentiation of epithelial processes/skeletal products lay in positional and/or temporal regulation of cellular activity and products. As cells produced at the colony margin migrated proximally, or as the colony margin advanced a predetermined distance, the mode and rate of inner epithelial secretion switched from high, continuous rates of growth and production of granular crystallites to slower, episodic growth rates, tabular crystallites and laminar skeleton.

Local discontinuities in the median lamina of *Peronopora* may be explained in terms of a growth rate model. Local discontinuities of the median lamina in *Peronopora* often occur in association with regions in which thin-walled ('endozonal') zooecial growth was prolonged (text-fig. 2). The recumbent zones of zooecia in these regions are also unusually long and lack cystiphragms (Boardman and Utgaard 1966, p. 1096). The periodic interruption of median granular layer formation was followed by relatively wide regions of endozonal growth. These widened endozonal regions occur not only at the base of young secondary fronds, but also periodically throughout frond growth along the margin of young fronds. Periodic prolongation of the relatively high growth rates typical of the recumbent zone and endozone is indicative of a colony-wide increase in growth rate. That a high growth rate was prolonged beyond its normal duration is also supported by the atypical lack of cystiphragms within the recumbent zones of the autozooecia in these regions. In other words, growth rate appears to have been high enough in these instances to have produced a relatively long recumbent region and some degree of endozonal growth before the first period of cystiphragm emplacement.

Rapid growth is energetically more expensive than slow or normal growth rates. Thus, if endozonal growth is indicative of high growth rates, the association of 'endozonal' growth with discontinuities in the median lamina suggests that there could have been a limited availability of energy for skeletal formation. High rates of growth along the colony margin may have precluded formation of the median lamina during limited periods of accelerated growth. The median lamina was formed during periods of normal growth. When growth rates increased, presumably energy that would otherwise have been allocated to median lamina formation was diverted to permit somewhat longer periods of 'endozonal' growth. Such an explanation could be considered a special case of generally poor developmental regulation of median lamina formation.

Diagenesis

The compositional differences between skeletal structures and the diagenetic matrix, coupled with the results of Sakagami *et al.* (1984), and readily interpretable astogenetic trends consistent with inferences based on alternative arguments suggest that elemental data could reflect real differences in the physiology of growth. Significant differences between the matrix and skeletal structures and among skeletal structures do not unequivocally demonstrate the absence of diagenetic alteration. However, the primary results of this study are consistent with independent predictions of compositional behaviour which would be expected in the relative absence, limited or differential influence of diagenesis on skeletal material and are consistent with inferences based on alternative

evidence. Further studies of this kind are warranted because they could contribute to knowledge about skeletal diagenesis, the physiology of skeletal growth and growth rates in extinct organisms.

CONCLUSIONS

The skeleton of *P. vera* contains Cu, Si, Fe, Mg, Mn, Yb, and Nb, many of which occur in concentrations significantly different from that of the zooecial void matrix. Ca density is inversely related to rates of skeletal growth and crystallite secretion. The density distributions of Ca and other trace elements among crystallite types, skeletal structures, and astogenetic growth zones support inferences concerning relative rates of crystallite secretion and skeletal growth based on alternative lines of evidence in bifoliate *Peronopora*. EDS data indicate differences in the rates of secretion and growth among crystallite types, acanthostyle cores, the median lamina, zooecial wall, and stages of zooecial ontogeny and colonial astogeny. Growth was most rapid within the granular skeleton of the median lamina and 'A-type' acanthostyles (paurostyles). Growth rate decreased from the median lamina through the recumbent zone, endozone, and exozone. Paurostyle cores were deposited more rapidly than endozonal wall but less rapidly than recumbent zone wall and the median lamina. Cu and Mn abundance distributions also support the succession of relative growth rates based on Ca data. Paurostyles contain more Cu than other structures. Mn is also most abundant in the median lamina and declined monotonically with reduced growth rate. Zones of disordered, irregular crystallites and laminar growth alternate in zooecial wall axes and are linked with increased secretion rates and increased episodicity, respectively during the cystiphragm/tabula emplacement cycle.

Results of this study are preliminary but suggest that compositional studies can provide information about relative rates of skeletal growth. The astogenetic growth rate curve derived from EDS data supports the results of growth curves based on an alternative method presented herein; intrazooecial cystiphragm frequency distribution per unit autozooecial wall length. A combination of these methods permits the reconstruction of astogenetic growth rates and their use as taxonomic descriptors. If differential growth rates can be identified on the basis of ultrastructural morphology, the evolution of skeletal wall microstructure and acanthostyle types may be interpreted in terms of heterochronic change.

The median lamina of bifoliate *Peronopora* is composed of one to three structures: 1, an outer laminar layer; 2, a medial granular layer; and 3, granular mesostyles. The mesostyles and medial layer are composed of smaller rhombic crystallites which have not been described in mesothecae of other stenolaemates. The median lamina is structurally continuous with the basal lamina but was not secreted against cuticle and is therefore interior-walled skeleton. Formation of the median lamina and paurostyle cores may be explained by differentiation of inner epithelium for high rates of secretion and growth. Local discontinuities in the median lamina can be explained by an energy budget-growth rate hypothesis.

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